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## Research paper

## Modern pollen rain and fungal spore assemblages from pasture woodlands around Lake Saint-Point (France)

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## ABSTRACT

Modern analogs are commonly used to investigate the relationships between modern pollen rain and the surrounding present vegetation and to improve our interpretation of fossil data. We collected modern pollen and spore rain in 18 more or less grazed and/or forested sites around Lake Saint-Point (Jura Mountains, France). Multivariate numerical techniques were applied to understand how modern pollen and non-pollen palynomorphs (NPP) taxa, collected in moss and dung samples, record local vegetation in the surroundings, and to identify indicators of tree cover or grazing. We show a strong relationship between current local herbaceous vegetation and pollen but underline the limits of past vegetation reconstructions based on AP/NAP ratio. In moss samples, we identified *Picea*, *Abies*, *Fagus* and *Corylus* pollen as well as *Trichocladium*, *Kretschmaria deusta* and *Cirrenalia* as indicators of tree cover. Spores of *Sporormiella* and some undetermined palynomorphs such as new NPP LCE-13 were positively correlated with openness while LCE-23 and LCE-32 could represent grazing indicators and/or coprophilous types. As compared to moss samples, dung samples contained much more pollen grains from *Trifolium repens*-type, *Trifolium pratense*-type, *Plantago lanceolata*-type and *Plantago major/media*-type taxa (grassland species eaten by cattle) and spores from coprophilous fungi.

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## 1. Introduction

There is a general agreement about the efficiency and reliability of studying modern pollen rains to reconstruct past vegetation. However, many factors such as interspecific variability in pollen productivity and dispersal, vegetation heterogeneity and atmospheric conditions, may influence pollen–vegetation relationships (Sugita, 2007): their non-linearity remains an important issue. The study of these relationships appears to be a major prerequisite to the interpretation of past pollen spectra (e.g. Heim, 1970; Gaillard et al., 1992, 1994; Hicks and Birks, 1996; Hjelle, 1997, 1998, 1999; Cour et al., 1999; Court-Picon et al., 2005; Gerasimidis et al., 2006; Mazier et al., 2006, 2008). With that aim in mind, identification of modern analogs is a common practice (Overpeck and Webb, 1985). Comparisons with the floristic composition of the plot enable to provide information about general pollen–vegetation relationships (e.g. Hjelle, 1997; Court-Picon et al., 2006; Mazier et al., 2006; Fletcher and Thomas, 2007; Cañellas-Boltà et al., 2009; Cugny et al., 2010; Montoya et al., 2010), and they are also used

to assess the degree of over/under-representation of a taxon in the pollen rain. In Northern Europe, several studies have been conducted to address pollen–vegetation relationships, for instance in Sweden (Gaillard et al., 1992; Broström et al., 1998), in Norway (Hjelle, 1997, 1999) and in northern Germany (Prager et al., 2006). Some studies have also been carried out in Scotland (Bunting, 2003), in England (Waller et al., 2005; Smith et al., 2010) and in arid environments in Spain (Carrion, 2002). However only few studies were interested in mountainous areas, such as the Pyrenees (Mazier, 2006; Cugny et al., 2010; Ejarque et al., 2011) and the French Alps (Court-Picon et al., 2005, 2006). Brun (2007, 2011) suggested to redefine the anthropogenic pollen indicators in low mountain areas of Franche-Comté (Jura Mountains), but mainly focused on arable-weed and ruderal flora from lowlands (up to 700 m a.s.l.) and did not account the specific characteristics of wooded-pastures, which are frequent at higher altitude in the Jura Mountains.

Regarding land use history, classical anthropogenic indicators, anthropocores as well as apophytes, are a well-grounded-tool to study human impacts (e.g. Behre, 1981, 1988; Berglund, 1991; Latałowa, 1992; Richard, 1995; Brun, 2011). Study of modern pollen rain may help to characterize different types of land use (Hjelle, 1999; Mazier et al., 2008). Comparisons between modern and past

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pollen rains have shown the need to take into account the specificity of each study area (e.g. Carrion, 2002; Brun et al., 2007; Cañellas-Boltà et al., 2009; Smith et al., 2010). Indeed, pollen rain–vegetation relationships are closely linked to landscape openness and morphology, human impact and climate. In the Jura Mountains, the semi-open landscape patchiness is at the origin of a very high vegetation heterogeneity and biodiversity (Mazier et al., 2008). Agriculture is therefore based on livestock and hay pasture, and these land use practices may affect the pollen rain–vegetation relationships. For instance, grazed pastures have a lower pollen productivity than mown areas, and the higher the pressure, the lower the pollen productivity is (Groenman-van Waateringe, 1993; Broström et al., 2004; Mazier et al., 2008). Furthermore, Court-Picon et al. (2005) showed that pollen spectra from open landscapes are likely to record pollen productivity from lower areas because of long-distance pollen transport, limiting the appropriateness between vegetation and modern pollen datasets. For example, some taxa such as *Pinus* and many of the arboreal taxa are well known to produce high quantities of pollen that can be found in modern moss samples far from the production source (Heim, 1970; Broström et al., 1998, 2004). In this respect, the models of pollen–vegetation relationships built for lowland areas cannot be applied to pollen assemblages in mountain areas.

Non-pollen palynomorphs (NPPs) have been recognized as good indicators of palaeoecological conditions and past human activities (van Geel, 2001, 2006). Although they bring a new interpretative dimension to palynological analysis without requiring more sampling and preparation (van Geel et al., 2003; Graf and Chmura, 2006), very few reconstructions of past vegetation and human activities combining both pollen indicators and NPPs have been carried out in mountainous areas (Mazier et al., 2009; Jouffroy-Bapicot, 2010; Ejarque et al., 2011). When regarding modern pollen spectra, NPPs are generally poorly considered; however, a few pioneer studies have investigated wetland, forested and/or mountain areas (Court-Picon et al., 2005; Barthelmes et al., 2006; Blackford and Innes, 2006; Prager et al., 2006; Cugny et al., 2010). These recent works brought new insights on the relationships between NPPs, vegetation and human activities. Coprophilous fungal spores, common in pollen slides, are for instance strictly local indicators of grazing pressure due to their low dispersal (van Geel et al., 2003; Blackford and Innes, 2006; Davis and Shafer, 2006; Gauthier et al., 2010; Laine et al., 2010). Furthermore, NPP assemblages found in pollen slides seem reliable when used as indicators of vegetation structure – including edges (Mulder and Janssen, 1999) – and of specific ecological conditions and substrates (Davis and Shafer, 2006; Prager et al., 2006) and their indicative value is also useful for environmental archeology (van Geel et al., 2003).

Our study aimed at providing a modern frame of reference taking into account the diversity of landscapes above 800 m a.s.l. in the Jura Mountains. Knowing that there is no arable land at this altitude, and that moss samples are very difficult to find in hayfields, we focused on pollen–NPP–vegetation relationships in the silvopastoral landscape surrounding Lake Saint-Point (Doubs, France), by analyzing 33 modern pollen spectra collected in moss and dung samples. This work was designed: (1) to compare vegetation data and modern pollen assemblages from different vegetation types from open pasture to ungrazed forest, (2) to identify pollen and NPP indicators of local tree cover and grazing pressure, (3) to identify new coprophilous fungi using 15 dung samples from grazed sites, and (4) to provide a frame of reference for the palynological results from Lake Saint-Point which may allow past vegetation reconstruction since 15,000 cal. BP (Leroux et al., 2008; Leroux, 2010; Magny et al., 2012).

## 2. Study area

Lake Saint-Point is a 7-km<sup>2</sup> lake located in the high chain of the Jura Mountains, with altitudes of its catchment (247 km<sup>2</sup>) ranging from

850 to 1463 m a.s.l. (Mont D'Or) (Leroux et al., 2008) (Fig. 1). The catchment area is under the influence of a semi-continental climate with cold winters and cool summers. Annual mean temperatures do not exceed 6.6 °C around Saint-Point and annual precipitation increases with altitude, from 1480 to 1810 mm per year. Although human presence is recorded around Lake Saint-Point since the Neolithic, strong human impact on vegetation is also shown for the Middle Age, with deforestation in the 9th century and the first occurrence of cultivated plants (cereals, *Cannabis*) and coprophilous fungi (such as Sordariaceae, *Sporormiella* and *Podospora*) later during the 13th century. Economy around Lake Saint-Point remains essentially based on animal breeding and cultivation of cereals until the 19th century. During the 20th century, cultures are progressively abandoned in favor of cattle rearing, which led to the expansion of Norway spruce (*Picea abies*). Except urban areas, the neighboring region of Lake Saint-Point is nowadays mainly represented by pasture-woodland landscapes. Current wood-pasture ecosystems inherit from past management, involving a complex scheme of interactions and feedback between biotic and abiotic compartments (Kohler et al., 2006; Gillet et al., 2010). Management of pasture woodlands results in a diversified set of land use, involving timber exploitation, cattle grazing and forage production. As a result, wooded pastures consist of mosaic of forests, wood-pastures, open grasslands and wetlands, where grazing pressure balances forest regeneration (Gillet and Gallandat, 1996a, 1996b).

## 3. Material and methods

### 3.1. Sampling design

In August and September 2009, 18 sampling sites distributed around Lake Saint-Point along a tree cover gradient have been selected from aerial photographs. In order to take into account the diversity of vegetation types around Lake Saint-Point and to provide modern-pollen analogs from open pastures to densely wooded pastures and forests, we used six types of sites (three sites per type): grazed wetlands (W), unwooded pastures (P0), sparsely wooded pastures (P1), densely wooded pastures (P2), grazed forests (P3) and ungrazed forests (F) (Fig. 2). This typology is derived from Gillet and Gallandat (1996b) and Gillet et al. (2002): our grazed wetlands and unwooded pastures presented a tree cover of 0%, sparsely wooded pastures from 15 to 40%, densely wooded pastures from 50 to 60% and grazed and ungrazed forests from 70 to 90% of tree cover.

Percentage cover of tree and shrub species was estimated within a 400-m<sup>2</sup> plot (20 m × 20 m) while herb species were identified in ten 0.25-m<sup>2</sup> quadrats (50 cm × 50 cm) within the 400-m<sup>2</sup> plot, so as to measure frequencies from presence/absence data. Five out of the ten quadrats were arbitrarily located to collect an epigeic moss sample; the five others were randomly located. For each station plot, the five moss samples were pooled in a single sample (from 1.9 to 9.9 g) for pollen analysis. Furthermore, one dung sample (named X<sub>n</sub><sup>D</sup>) was collected in each of the 15 grazed sites (from 5.2 to 18.2 g), within a dung pat to avoid secondary aerial pollen signal. Except W<sub>a</sub>, which was grazed by horses, all grazed sites were grazed by cattle. Grazing was confirmed by presence of dung pats or evident from the presence of grazing animals in the field.

### 3.2. Laboratory methods and pollen analysis

Chemical treatments on moss and dung samples followed Sittler (1955) and Delcourt et al. (1959). Organic matter was dissolved by soda (NaOH) and samples were sieved to remove components larger than 200 µm. Fluorhydric acid (HF, 40%) was used to dissolve silicates. A solution of 90% of acetic anhydride (C<sub>4</sub>H<sub>6</sub>O<sub>3</sub>) and 10% of sulphuric acid (H<sub>2</sub>SO<sub>4</sub>) was added and samples were warmed up at

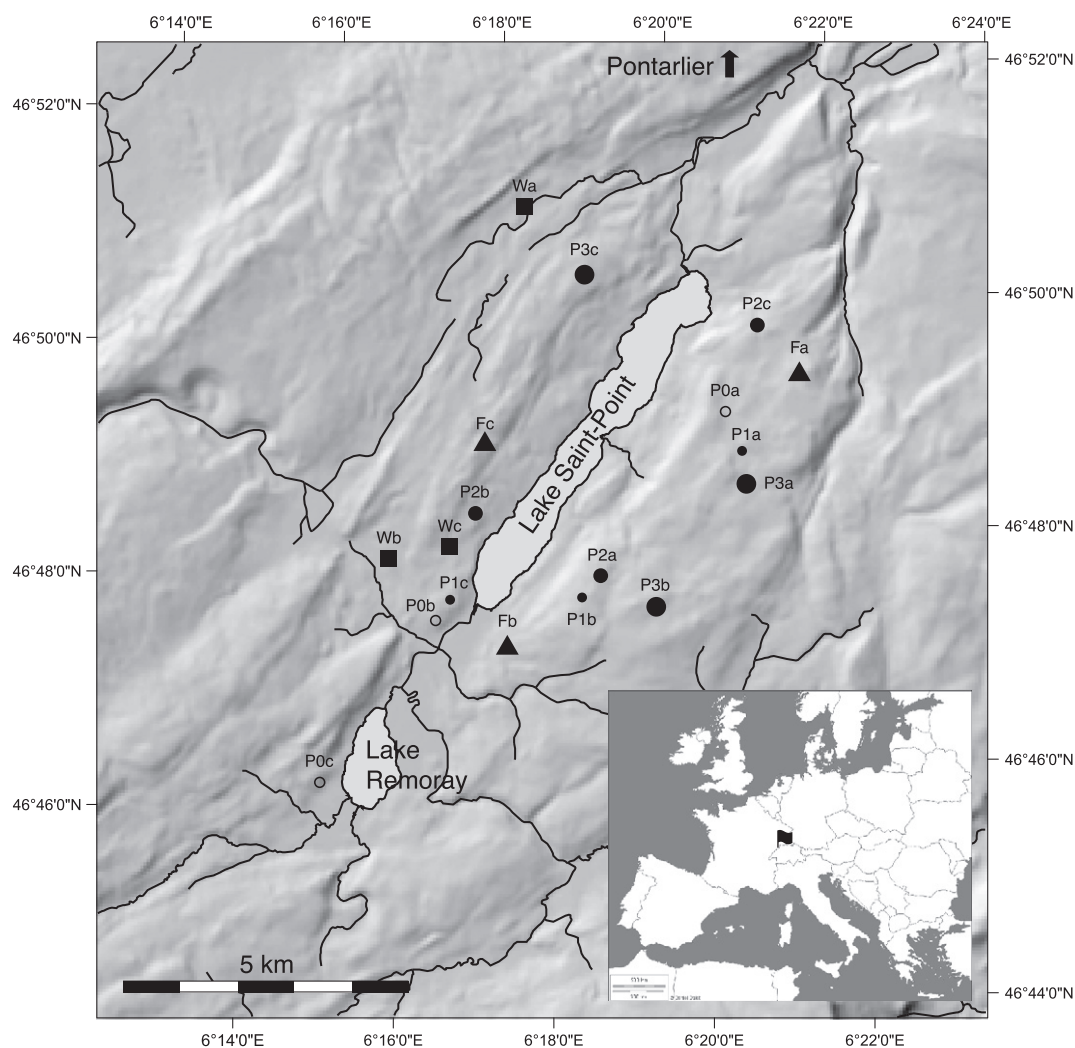


Fig. 1. Location of the 18 study sites around Lake Saint-Point.

80 °C for 8 min. Sediments were finally put in Eppendorf tubes and covered with glycerine ( $C_3H_8O_3$ ).

### 3.3. NPP counting

Each pollen, spore and NPP type is usually expressed as a percentage of total land pollen (van Geel et al., 1981). Some authors try to count a minimum of 100 fungal spores per sample before calculating percentages (Blackford and Innes, 2006). In our study, we tried to optimize the counting method regarding NPPs in order to find the best compromise between effort and precision. We selected five contrasting samples (out of 33) that differed in NPP density, on which we counted 15 lines. Lines can be seen as bands, thus NPPs were counted over about 50% of the total slide area. Taxa were counted independently for each line, allowing the use of species pool estimation methods (Fig. 3). Mean species accumulation curves were drawn by randomly permuting the data (Gotelli and Colwell, 2001).

As a result, 80% of the estimated total pool of NPP taxa was reached when counting 8 lines for  $W_c$ , 10 for  $P2^D$  and  $P3_b$ , and 13 for  $P0_c$ , while 15 lines were not sufficient for  $P3_a^D$  (vertical dashed lines in Fig. 3). Finally, we chose to count only six bands because of time limitation. Nevertheless, this limit corresponds to 20% of the total slide area and led to a count sum higher than 200 NPPs for 21 of the 33 samples. We still need more statistical investigation to

optimize the counting method, particularly for samples offering high pollen richness but low amounts of NPP counts.

### 3.4. Counting method

Each of the 33 samples (18 moss samples and 15 dung samples) was mounted on slide and both pollen grains and NPPs were identified and counted using a photonic microscope, following identification keys in Beug (2004) and pictures and descriptions in van Geel and Andersen (1988), van Geel et al. (2003), van Geel and Aptroot (2006) and Cugny et al. (2010), respectively. In accordance with Nakagawa et al. (1998), a minimum of 400 terrestrial pollen grains has been counted for each sample, except for samples  $P0_a$  (168 pollen grains),  $P0_a^D$  (229) and  $W_c$  (314) as pollen preservation was problematic in the two moss samples. NPPs have been counted independently on six lines according to a preliminary analysis. NPP nomenclature follows current common rules: “HdV-xxx” (types from van Geel, Hugo-de-Vries Laboratory, University of Amsterdam, The Netherlands), “TM-xxx” (types from Cugny et al. (2010) and Cugny (2011), University of Toulouse Le Mirail, France). Unknown and potential new types have been given codes such as “LCE-xxx” (LCE for Laboratoire Chrono-Environnement, University of Franche-Comté, France).

Because *Lycopodium* tablets (or other methods involving the addition of a marker pollen) were not available in our facilities at this time, pollen



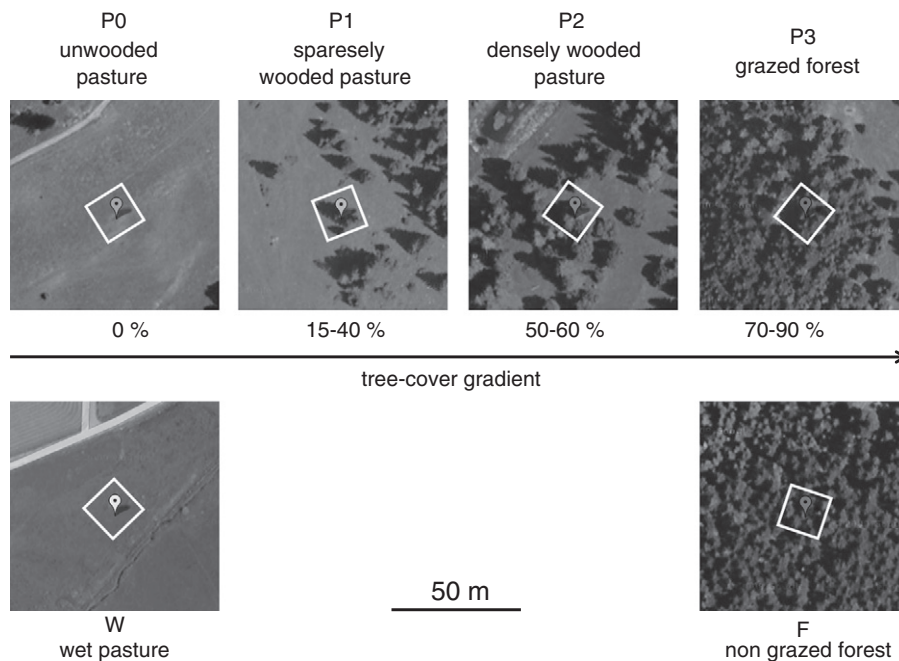


Fig. 2. Examples of sites selected according to tree cover, grazing and moisture. White squares represent the location of the 400-m<sup>2</sup> chosen as examples.

concentration was calculated using a volumetric method (Cour, 1974) (expressed for 1 g of moss or dung) following the equation:

$$N_{ij} = \frac{n_{ij} w_j V_j}{k_{ij} F v_j m_j}$$

$N_{ij}$	relative concentration of taxon $i$ in sample $j$ per sample gram ( $g^{-1}$ )
$n_{ij}$	absolute count of taxon $i$ in sample $j$
$w_j$	slide width (as two types of slides were used: 22 and 24 mm width)
$k_{ij}$	number of lines read above slide (six for NPP taxa, variable for pollen taxa)
$F$	width of field of view (mm)
$V_j$	total volume of sediments ( $\mu$ l) after preparation
$v_j$	volume of sediments spread on slide ( $\mu$ l)
$m_j$	mass of collected sample (g)

### 3.5. Statistical analyses

Multivariate numerical methods are commonly used to assess how vegetation is recorded in pollen assemblages (Prentice, 1980; Guiot, 1990; Gaillard et al., 1994; Broström et al., 1998; Gavin et al., 2003; Court-Picon et al., 2005; Sugita, 2007). We applied several multivariate analyses to our modern palynological and vegetation

data in order to investigate pollen–NPP–vegetation relationships around Lake Saint-Point. All analyses were performed using R software, version 2.13.1 (R Development Core Team, 2011).

At first, we applied a Multiple Factor Analysis (MFA) to the moss sample dataset to symmetrically relate homogeneous groups of descriptors (Escoufier and Pagès, 1994; Bécue-Bertaut and Pagès, 2008; Borcard et al., 2011), using the R package *FactoMineR* (Lê et al., 2008; Husson et al., 2010). Among the variety of symmetric ordination methods that are available for the linking of ecological data tables, MFA was chosen because it allows the simultaneous coupling of several groups or subsets of variables defined on the same objects. MFA is a simple variant of co-inertia analysis, which seeks the common structures present in all or some of these subsets. Contrary to asymmetric constrained ordination methods, such as CCA (Canonical Correspondence Analysis) or RDA (Redundancy Analysis), MFA does not assume a priori any causal relationship among variables, and can be applied to datasets where the number of objects is very low as compared to the number of descriptors in each group (Dray et al., 2003). The similarity between the geometrical representations derived from each group of variables is measured by the RV-coefficient, ranging from 0 to 1 (Escoufier, 1973; Robert and Escoufier, 1976). RV-coefficients can be tested by permutations (Josse et al., 2008). We considered nine groups of variables: (1) two numeric environmental variables (altitude, tree cover); (2) two categorical environmental variables (vegetation type, presence of grazing); three groups of vegetation

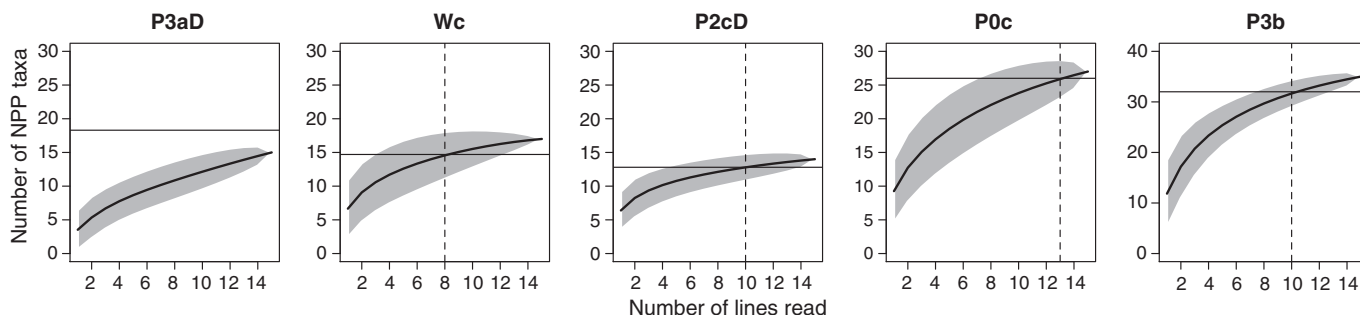


Fig. 3. Taxa pool estimation for five selected samples, with 95% confidence interval. Abscissa gives number of counted lines; ordinate gives taxa richness. Horizontal line shows 80% of estimated total pool.

data, for (3) tree, (4) shrub and (5) herb layers; three groups of pollen data, for (6) tree, (7) shrub and (8) herb taxa; (9) NPP data. We applied Hellinger transformation separately to each group of taxa (i.e. groups 3 to 9) to account for the double-zero problem (Legendre and Gallagher, 2001), and numeric environmental variables were standardized. The whole dataset encompassed 326 variables.

We then performed a Redundancy Analysis (RDA) using *vegan* R package (Oksanen et al., 2010) to assess the response of pollen and NPP assemblages to two explanatory variables: tree cover and sample type (moss or dung). Pollen–NPP concentration data were Hellinger-transformed prior to the analysis. The dataset used for RDA encompassed 171 response variables and two explanatory variables.

### 3.6. Drawing methods for pollen and NPP diagrams

Pollen and NPP diagrams for moss and dung samples were drawn using TILIA and TGView software (Grimm, 1991). Pollen taxa are expressed in percentages relative to the pollen sum. The pollen sum includes all pollen taxa except Cyperaceae and Poaceae. Although this is not usual, we chose to exclude Poaceae because of the high values they would otherwise reach: up to 50% of total pollen counts in moss samples and up to 95% in dung samples from less wooded stations. Taxa with very low values and/or rare taxa are excluded from diagrams and gathered in Appendices A and B for moss and dung samples, respectively. Taxa are grouped according to their life form and ecology: trees, herbs, tree cover related NPPs (van Geel and Aptroot, 2006), coprophilous fungi (van Geel and Aptroot, 2006; Cugny et al., 2010), NPP taxa without very precise ecology, NPP types with an unknown ecology (van Geel, 1978; Pals et al., 1980; van Geel et al., 1981; van Geel and Aptroot, 2006; Cugny et al., 2010) and new NPP types.

## 4. Results

### 4.1. Vegetation around Lake Saint-Point

Appendix C shows the vegetation relevés from 18 stations distributed around Lake Saint-Point. Unwooded pastures and grazed wetlands are characterized by the absence of trees and a very sparse shrub layer. Only 1% of the 400-m<sup>2</sup> plot was covered by *Rosa arvensis* in site PO<sub>a</sub> and 2% by *Salix cinerea* in sites W<sub>b</sub> and W<sub>c</sub>. The herb layer is mainly composed of species of Poaceae, Apiaceae, Asteraceae, Fabaceae, and Ranunculaceae, as well as some *Plantago* species in unwooded pastures. Grazed wetlands mostly differ from unwooded pastures by the presence of some hygrophilous species such as *Cirsium palustre*, *Epilobium palustre*, *Equisetum palustre*, *Galium palustre*, *Galium uliginosum*, *Geum rivale*, *Juncus alpinoarticulatus*, *Mentha aquatica* and *Valeriana dioica*. Sparsely wooded pastures are characterized by the presence of some trees (*Picea abies*, from 15 to 40% cover) and few shrubs, mainly *Corylus avellana*, *Crataegus monogyna*, *Lonicera xylosteum* and *Rubus fruticosus* aggr. They exhibit similar herb species, in addition to some undergrowth ones such as *Fragaria vesca*. Densely wooded pastures show more of these understory species, e.g. *Carex sylvatica* and *Geranium robertianum*, because of the presence of more trees and shrubs. Some taxa are almost absent in forests while they are well represented in other vegetation types: *Achillea millefolium*, *Agrostis capillaris*, *Alchemilla monticola*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca rubra* aggr., *Ranunculus nemorosus*, *Trifolium pratense* and *Trifolium repens*. On the other hand, *Galium odoratum*, *Oxalis acetosella* and *Polygonatum verticillatum* are exclusively present in forests.

### 4.2. Pollen and NPP diagrams

Modern pollen spectra (Fig. 4) showed a local pollen rain with a dominance of *Fagus*, *Abies* and *Picea* in forested sites (up to 20.1, 38.6

and 33.2% of pollen sum, respectively). *Quercus* and *Carpinus*, completely absent in the local vegetation, belong to the regional pollen rain (up to 11.2% in F<sub>b</sub> and 7.8% in W<sub>b</sub>, respectively). Few occurrences of very long-distance pollen transport from south Europe or the Rhône river valley (e.g. *Ambrosia*) were recorded in the moss samples. NPPs, and particularly fungal remains, are known to have a strictly short dispersal distance, so they are of very local origin (van Geel, 2001; van Geel et al., 2003; Blackford and Innes, 2006; Graf and Chmura, 2006; van Geel and Aptroot, 2006; Cugny et al., 2010). As expected, local tree pollen percentages tended to increase with tree cover, whereas herbaceous pollen and pasture-dependent NPP abundances decreased. However some tree taxa such as *Fagus*, *Pinus* and *Quercus* were able to reach high values in grazed wetlands (up to 19.2, 16.4 and 8.8% of pollen sum, respectively), where the open vegetation allowed a more regional signal. Hygrophilous taxa (such as *Filipendula*) as well as Cyperaceae showed highest percentages in grazed wetlands. Ranunculaceae and *Apiosordaria verruculosa* (HdV-169) also reached higher percentages in such wet sites. Among the NPPs, *Anthostomella fuegiana*, *Assulina muscorum*, *Trichocladium*, *Cirrenalia* and *Kretschmaria deusta* (HdV-44; formerly known as *Ustilina deusta*) were strongly limited to the most wooded sites. Coprophilous fungi (*Apiosordaria*, *Arnium*, *Cercophora*, *Podospora*, Sordariaceae, *Sporormiella*) did not reach high values in ungrazed forests and in densely wooded pastures.

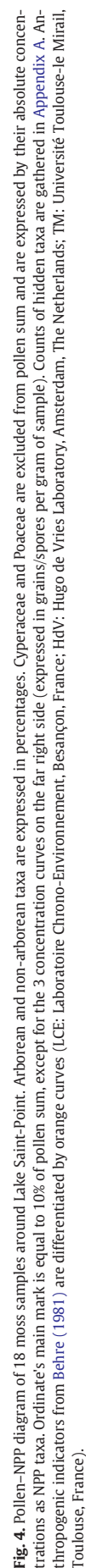
By contrast, dung samples (Fig. 5) showed very low percentages of tree pollen (except *Corylus*, which reached 40% in sample P2<sub>b</sub>) but greater proportions of herb pollen and spores of coprophilous fungi such as Sordariaceae and *Sporormiella*. Additionally, the contribution of herbaceous taxa increased along the openness gradient. Exceptions were Ranunculaceae and *Trifolium repens*-type. As in the moss samples, Cyperaceae and *Filipendula* reached their respective highest amounts in grazed wetlands (W). Tree cover related NPPs showed the same low untrended proportions as tree pollen.

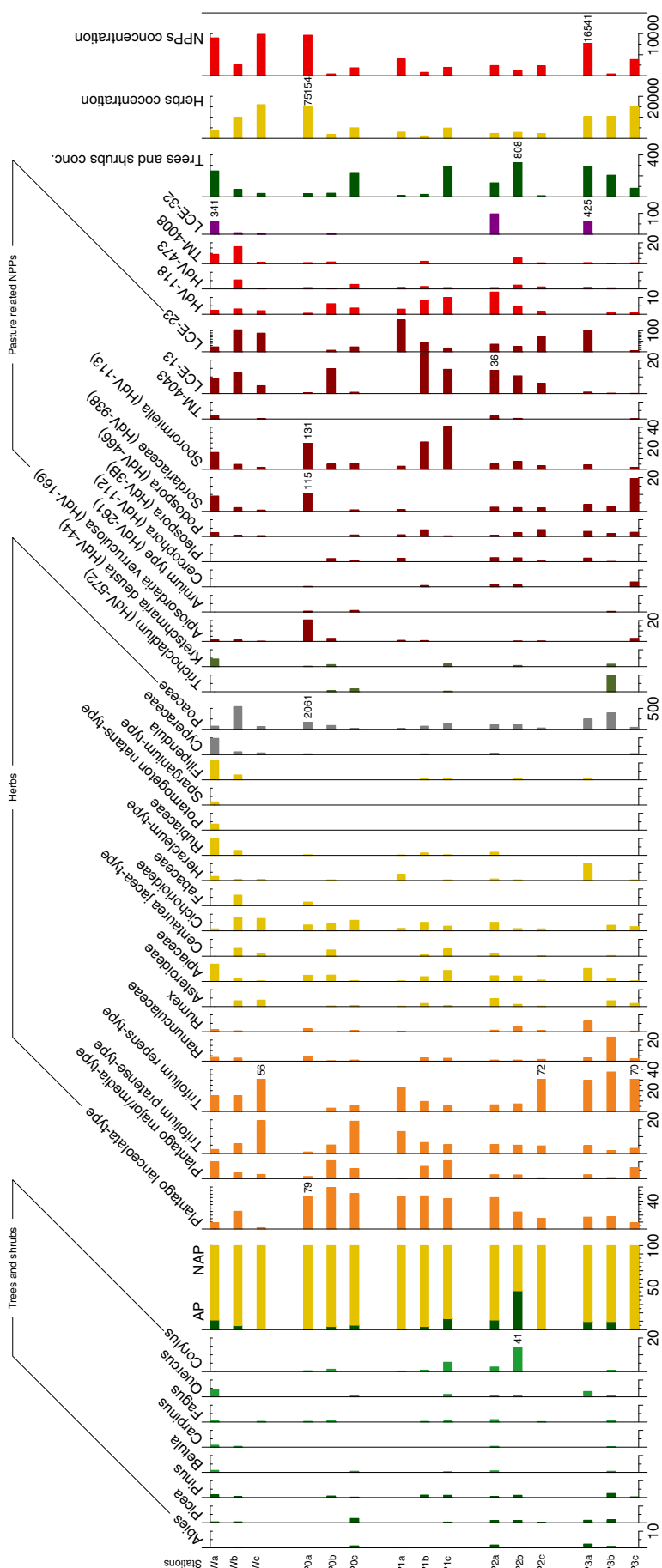
Figs. 4 and 5 also present some selected potential new NPPs like LCE-12, LCE-13 and LCE-23. An illustration of some of these NPPs is given in Fig. 8, and a short morphological description is given for each of the 21 potential new NPPs (Appendix D).

### 4.3. Multiple Factor Analysis

The two first axes accounted for 40% of the variance of the MFA global analysis of the moss samples. In the factorial map of the two first axes (Fig. 6), moss samples were clearly distributed along a gradient of tree cover, with a good segregation of the six vegetation types.

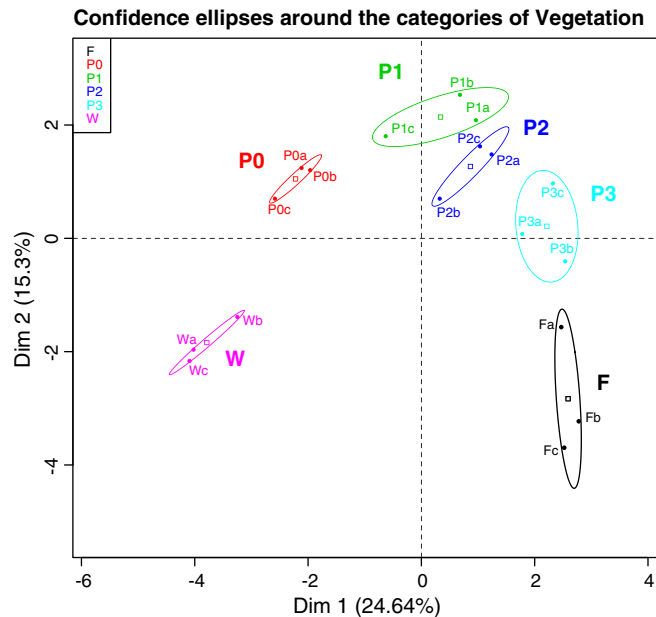
Table 1 gathers values of RV coefficients for every pair of groups of variables and their significance according to permutation tests. These tests were not available (na) for pairs including Env2 as this group consists of categorical variables. Strong and significant relationships were found between group Env1 and almost all the other groups, in particular with shrub (VegS) and herb (VegH) species and with NPPs (NPP). The group NPP also shares significant RV coefficients with all other groups of variables (up to 0.785 with group VegH), except with the group of shrub pollen taxa (SP). Another interesting point to note is the high and significant RV coefficient between the group of herb species (VegH) and the group of herbaceous pollen taxa (HP). No significant relationship was found between tree species and arboreal pollen nor between shrub species and shrub pollen. The group of shrub species (VegS) shows high and significant RV coefficients with both groups of tree species and herb species, and with both groups of arboreal and herbaceous pollen taxa as well. In addition, the group of tree pollen taxa has relatively low but significant RV coefficients with both groups of herb species and herb pollen taxa.





**Fig. 5.** Pollen–NPP diagram of 15 dung samples around Lake Saint-Point. Arboreal and non-arboreal taxa are expressed in percentages. Cyperaceae and Poaceae are excluded from pollen sum and are expressed by their absolute concentrations as NPP taxa. Ordinate's main mark is equal to 10% of pollen sum, except for the 3 concentration curves on the far right side (expressed in grains/spores per gram of sample). Counts of hidden taxa are gathered in Appendix B. Anthropogenic indicators from Behre (1981) are differentiated by orange curves (LCE: Laboratoire Chrono-Environnement, Besançon, France; HdV: Hugo de Vries Laboratory, Amsterdam, The Netherlands; TM: Université Toulouse-le Mirail, Toulouse, France).





**Fig. 6.** Projection of axes 1 and 2 of the Multiple Factor Analysis of the moss samples. Ellipses represent 95% confidence intervals around the centroid for each vegetation type.

#### 4.4. Redundancy analysis

We performed a RDA to reveal the response of modern pollen and NPP composition to tree cover and sample type (moss or dung) and identify taxa specific to these variables. The explanatory variables explained 36.2% of the total variance of the pollen–NPP dataset (adjusted  $R^2 = 31.9\%$ ,  $P = 0.001$ , 999 permutations). As shown in Fig. 7a, this model succeeded very well in sorting moss samples along a tree cover gradient, contrary to dung samples, which were clearly grouped on the right side of the first axis. Grassland pollen taxa such as *Trifolium pratense*-type, *Trifolium repens*-type, *Plantago lanceolata*-type, *Plantago major/media*-type, and Poaceae, as well as NPP spores LCE-32 and LCE-23 (Fig. 8) were mostly found in dung samples (Fig. 5). From

**Table 1**

RV coefficients among groups of variables used in the Multiple Factor Analysis of the moss samples. Env1: 2 numerical environmental variables; Env2: 2 categorical environmental variables; VegT: 7 plant species in the tree layer; VegS: 25 plant species in the shrub layer; VegH: 133 plant species in the herb layer; AP: 16 arboreal pollen taxa; SP: 13 shrub pollen taxa; HP: 60 herbaceous pollen taxa; NPP: 82 non-pollen palynomorph taxa.  $P$ -value:  $0.1 \geq > 0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$ . Permutation tests are not available for categorical variables (na).

	Env1	Env2	VegT	VegS	VegH	AP	SP	HP
Env2	0.381	na						
VegT	0.307	0.429	na					
VegS	0.535	0.539	0.516	na				
VegH	0.557	0.699	0.355	0.599	na			
AP	0.367	0.372	0.295	0.552	0.426	na		
SP	0.270	0.190	0.118	0.167	0.226	0.174	na	
HP	0.308	0.553	0.326	0.483	0.563	0.433	0.321	na
NPP	0.670	0.617	0.429	0.649	0.785	0.511	0.264	0.512

the side of moss samples, several tree and shrub pollen taxa, such as *Picea*, *Abies*, *Fagus* and *Corylus*, were strongly associated with high tree cover, as well as *Trichocladium* (HdV-572), HdV-118, and in some extent *Kretschmaria deusta* (HdV-44), *Cirrenalia* and *Assulina muscorum* (HdV-32A); while *Sporormiella* (HdV-113) and LCE-13 are shown opposed to tree cover.

## 5. Discussion

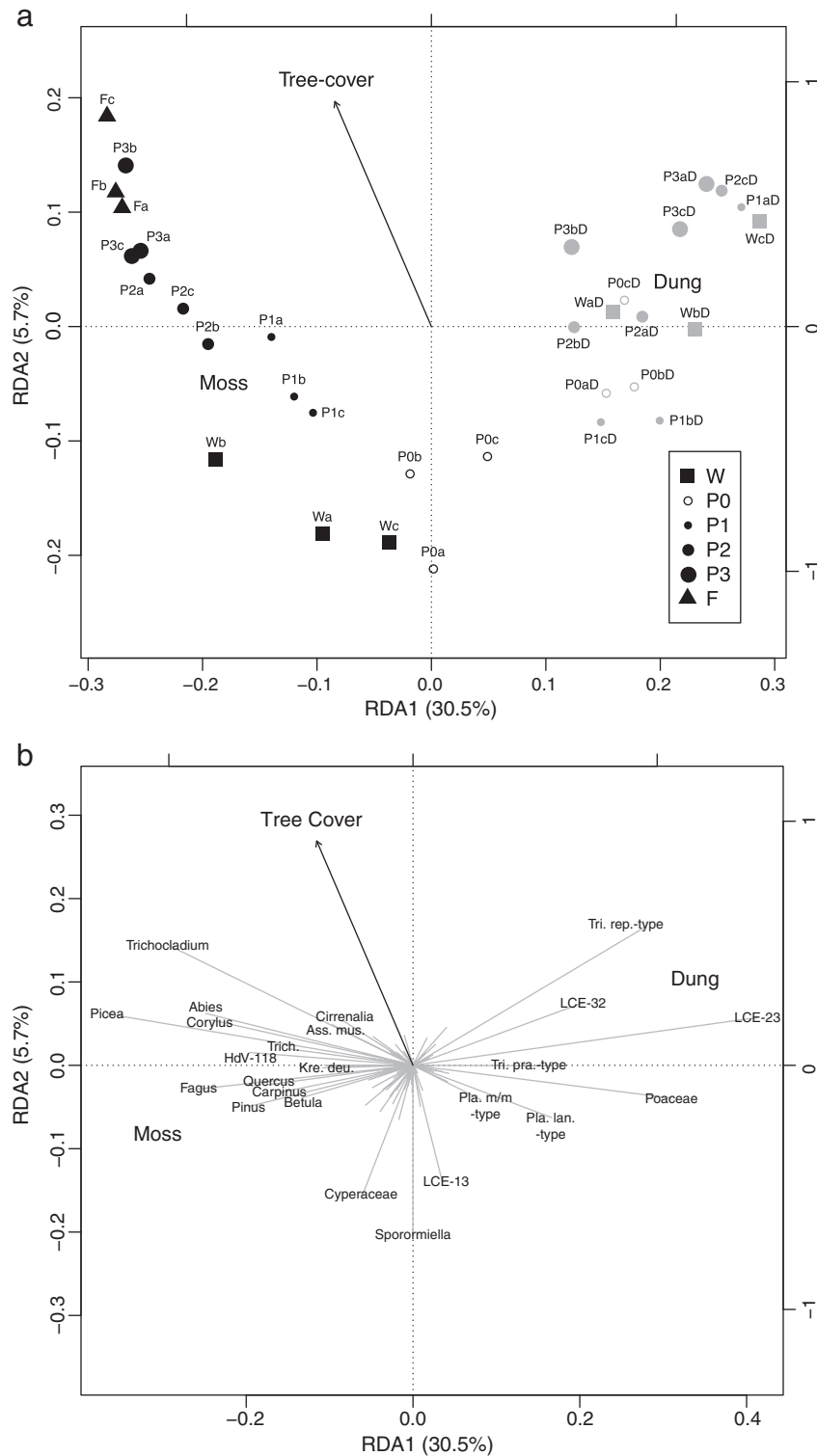
### 5.1. Relationships between vegetation, moss and dung samples, pollen and NPP assemblages

As shown by previous studies (e.g. Court-Picon et al., 2005), variations in pollen assemblages are related to vegetation type with an increase in tree pollen and tree-dependent NPPs in forested sites, a dominance of herb pollen in open landscapes, and occurrence of coprophilous fungi in grazed sites. Additionally, hygrophilous taxa indicate wet conditions around the sampling plot (e.g., *Filipendula* and Ranunculaceae and Cyperaceae to some extent). In fact these taxa reach their highest values in grazed wetland sites.

We collected dung samples to specifically investigate the signal of coprophilous fungi. We found that these taxa reached high values in dung samples (up to 40 spores of *Arnium*-type, 3986 spores of Sordariaceae and 4566 spores of *Sporormiella* per gram of dung from unwooded pastures, and up to 300 spores of *Cercophora* and 259 spores of *Podospira* per gram of dung from grazed forests—that corresponds respectively to 0.9, 114.6, 131.3, 2.9 and 2.5% relatively to the pollen sum). However, they did not show a clear response to tree cover. Actually, coprophilous fungi may find basically every nutrient they need in the dung pat, regardless to vegetation openness. Some pollen taxa, such as *Plantago lanceolata*-type and *Trifolium pratense*-type, were particularly abundant in dung pats. The first species occurs frequently in pastures and produces an abundant pollen rain: a single anther of *Plantago lanceolata* produces between 15,700 and 29,500 pollen (Richard and Géry, 1993) so it is not surprising to find it in dung. *Plantago lanceolata*, because of its high pollen productivity, may also be overrepresented in moss samples (Broström et al., 2008). The second species, pollinated by insects, is also common in pastures, but rarely occurs in pollen diagrams. Its over-representation in dung samples is undoubtedly linked to its ingestion by cattle. This is in agreement with Carrion (2002) who showed that pollen spectra from dung represent the material selected by cattle, from a local area. However, both local and regional pollen rains may be present on each leaf portion ingested by herbivores. Taxa such as *Quercus* and *Carpinus*, coming from the regional pollen rain, occur with low percentages in dung but are absent from the local area. The coprophilous fungi recorded in the samples grew in dung pats, but they could also have been ingested, if wind-dispersed ascospores were present on the grazed plants (Aptroot and van Geel, 2006).

Dimension 1 of the MFA sorted moss samples according to a tree cover gradient, and dimension 2 allowed distinguishing grazed wetlands and ungrazed forests from wood-pastures (Fig. 6). In fact, axis 1 (related to tree cover) did not clearly separate these categories from their wood-pastures equivalent (P0 for W and P3 for F) but axis 2 did show their differences. Our unbalanced design regarding the presence of grazing and the lack of information about grazing intensity did not allow a specific assessment of the response of pollen–NPP rain to grazing pressure. However, tree cover and grazing pressure being negatively correlated (Buttler et al., 2009), modern analogs could be used to interpret fossil pollen–NPP data regarding both environmental conditions.

RV coefficients (Table 1) highlighted an important link between environmental gradients derived from group Env1 (altitude and tree cover) and compositional gradients in the shrub and herb layers. As tree cover was the variable we chose for the stratification of sampling sites, we might also expect a strong link between this group and the



**Fig. 7.** Projection of axes 1 and 2 of the Redundancy Analysis of the moss and dung samples. a: Samples (scaling 1); b: taxa (scaling 2). Only taxa far from the origin are labeled (Trich.: *Trichoglossum* cf. *hirsutum* (HdV-77B); Ass. mus.: *Assulina muscorum* (HdV-32); Kre. deu.: *Kretschmaria deusta* (HdV-44); Pla. lan.-type: *Plantago lanceolata*-type; Pla. m/m-type: *Plantago major/media*-type; Tri. rep.-type: *Trifolium repens*-type; Tri. pra.-type: *Trifolium pratense*-type; LCE: Laboratoire Chrono-Environnement, Besançon, France; HdV: Hugo de Vries Laboratory, Amsterdam, The Netherlands).

group of tree species, which directly contributes to the tree cover, but this is not the case. Although most wooded sites are distributed in a higher altitude range than unwooded sites, this result probably suggests a change in tree species composition rather than a general tree cover increase with altitude. Indeed, while *Corylus avellana*,

*Crataegus monogyna*, *Fagus sylvatica*, *Fraxinus excelsior*, *Sorbus aucuparia* and *Acer pseudoplatanus* showed low percentages of cover regardless of altitude (within our study's range, i.e. from 800 to 1200 m a.s.l.), *Abies alba* and *Picea abies* generally reached higher percentages in the highest sites.



**Fig. 8.** NPP plate. a: LCE-23. b: *Thecaphora*. c: LCE-24. d: *Sporormiella* (HdV-113). e: HdV-55. f: *Cirrenalia*. g: *Trichocladium*. h: TM-4043. i: *Scopinella* (HdV-343). j: TM-4008. k: LCE-12. l: LCE-13. m: *Apiosordaria* (HdV-169). n: LCE-26. o: HdV-85. p: *Dictyosporium* (HdV-498). q: *Sordariaceae* (HdV 55a). r: LCE-27. s: *Geoglossum sphagnophilum* (HdV-77A). t: HdV-351. u: *Assulina muscorum* (HdV-32A). v: LCE-15 (LCE: Laboratoire Chrono-Environnement, Besançon, France; HdV: Hugo de Vries Laboratory, Amsterdam, The Netherlands; TM: Université Toulouse-le Mirail, Toulouse, France).

RV coefficients evidenced not only the strong link of NPP assemblages with environmental conditions (altitude and tree cover, related to grazing pressure) but also with shrub and herb species assemblages. This strongly suggests that NPPs provide useful indications complementing pollen data, in agreement with early and more recent studies on NPPs (e.g. van Geel, 1978; Sherwood-Pike, 1988; van Geel, 2001; van Geel et al., 2003; Graf and Chmura, 2006; van Geel, 2006).

RV coefficients also provide insight to the relationship between current vegetation composition and pollen spectra after distinguishing shrub and arboreal pollen taxa, which are usually gathered in a single

group. Despite the fact that MFA did not return any significant RV coefficient between tree species and arboreal pollen taxa or between shrub species and shrub pollen taxa, it did show a significant relationship between herb species and herbaceous pollen taxa. The absence of a significant link between the two tree groups and between the two shrub groups could be due to a high pollen production and dispersal from these taxa, leading to a background pollen signal of trees and shrubs that smoothes the differences between our vegetation types and inhibits the MFA to underline a strong link between these groups. Moreover, Fig. 4 shows that open sites are likely to express important



proportions of arboreal and shrub taxa, more specifically in wetlands. This mainly concerns *Fagus*, which is present in our study area (*Fagus sylvatica*) but not as a dominant species, and secondarily *Pinus*, *Carpinus* and *Quercus*, which are not currently present locally. However, knowing that most fossil anthropogenic indicators consist of herb taxa (e.g. pollen of cereals and weeds), the lack of relationship between local woody species and the pollen assemblages records should not prevent further interpretation of fossil records to reveal human impact on past vegetation.

In addition, the group of shrub species is also strongly linked to the group of arboreal pollen taxa. This could be because the same woody species may belong to different layers in the vegetation relevés but not in the pollen records, since it is not possible to know whether an arboreal pollen grain was produced by a mature tree or by a small one in the shrub layer.

## 5.2. Identification of potential indicators

Our results allow us to suggest several potential tree cover, vegetation openness and grazing indicators. First, we can report some tree cover indicators. Pollen grains and NPPs found in dung pats were partly previously ingested by herbivores (Bell, 1983; Carrion, 2002; Aptroot and van Geel, 2006). As a consequence, dung-sample results were likely to overestimate herbaceous pollen signal and underestimate the arboreal group, and RDA did not clearly reveal a tree cover gradient among dung samples. However, it did among moss samples, showing *Picea*, *Abies*, *Fagus* and *Corylus* pollen taxa in moss samples closely related to tree cover and suggesting to consider them as local indicators of forested areas. Indeed *Picea abies* and *Abies alba* were the main tree species in our vegetation relevés, contributing the most to tree cover in wooded sites, while *Fagus sylvatica* and *Corylus avellana* were the main underwood shrub species.

NPPs offer additional potential indicators. *Kretschmaria deusta* (HdV-44) is reported in a diversified range of tree hosts in Northern Europe (*Abies*, *Acer*, *Aesculus*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Fagus*, *Fraxinus*, *Populus*, *Quercus*, *Salix*, *Taxus*, *Tilia* and *Ulmus*) (van Geel and Aptroot, 2006). Except *Aesculus*, *Populus* and *Taxus*, all these taxa were also found in the pollen assemblages, and many of them were represented in our vegetation survey (*Abies alba*, *Acer pseudoplatanus*, *Fagus sylvatica* and *Fraxinus excelsior*). *Kretschmaria deusta* has also been described as a very local tree cover indicator (van Geel and Andersen, 1988) but it seems it can occur in sites at a 100 m distance from forests (Cugny et al., 2010). Recent results suggest that it could be related to the occurrence of beech (Cugny et al., 2010). At our study sites, most trees are conifers (*Picea abies* and *A. alba*) which could explain why *K. deusta* did not appear very clearly as a tree cover indicator. RDA showed three other NPP taxa positively related to tree cover and negatively to vegetation openness, namely *Trichocladium* (HdV-572), *Assulina muscorum* and *Cirrenalia* (Fig. 8). *Trichocladium* is known as a dominant taxon in beech forests but was also found in oak forests (Cugny et al., 2010). Here it seems more ubiquitous and it could turn out to be a good tree cover indicator. Thecamoeba *A. muscorum* is commonly reported in peat and *Sphagnum* samples (Charman et al., 2000; Cugny et al., 2010) but its apparent tree cover indicative power is likely to be due to its absence in unwooded and sparsely wooded sites and to the huge amount found in one ungrazed forest site. It has also never been found in dung samples. Therefore, *A. muscorum* should more likely be considered as an indicator of a moss habitat. Finally, *Cirrenalia* was here shown to be related to tree cover, in agreement with Cugny (2011) and Gelorini et al. (2010).

Some NPPs could be described as indicators of vegetation openness and grazing, namely *Sporormiella* (HdV-113) and LCE-13 (Fig. 8). *Sporormiella* is known as a strictly local grazing pressure indicator (Blackford and Innes, 2006; Davis and Shafer, 2006) and is commonly

used for past grazing pressure reconstruction (van Geel et al., 2003; Gauthier et al., 2010). Here it also seems to be related to open environments, as well as LCE-13, as evidenced by their opposite position to tree cover in RDA despite its small occurrence in ungrazed station F<sub>a</sub>.

Taxa found in dung samples could also be used as potential grazing indicators. Sordariaceae, *Podospora* and *Pleospora* are coprophilous fungi usually reported as pasture indicators. Indeed they were observed in dung samples, as well as TM-4043 (Cugny et al., 2010; Cugny, 2011) and especially LCE-23. We found high amounts of LCE-23 and almost exclusively in dung samples. We found LCE-32 exclusively in dung samples as well, in high quantities, but only in 6 of the 15 dung samples, from wetlands, unwooded or densely wooded pastures. *Plantago lanceolata*-type pollen is traditionally interpreted as an indicator of grazing pressure (Court-Picon et al., 2005) and here it appeared negatively related to tree cover. *Plantago lanceolata*-type, *Plantago major/media*-type, *Trifolium pratense*-type and especially *Trifolium repens*-type are other grassland taxa that we found in higher quantities in dung samples than in moss samples. They are often reported as pasture indicators (Behre, 1981). Indeed, the plant species they represent (*P. lanceolata*, *P. major*, *P. media*, *T. pratense*, *T. repens* and *T. dubium*) were more frequent in the less wooded grazed sites. *Trifolium repens*-type could directly represent (together with Poaceae) most of the cattle diet.

Some other unknown and potentially powerful indicators may remain among our dataset, as identifying a non-pollen palynomorph at the species or the genus level is rarely possible (Prager et al., 2006). Moreover, a single morphotype can come from different taxa and a single taxon can produce several different morphotypes. For these reasons a precise morphological definition of types and a clear distinction between NPPs truly described as novel types and those considered as possible duplicates of types described in previous studies would be very helpful to allow NPP counting to reach its full potential (Joosten and de Klerk, 2002).

## 5.3. Spatial and temporal scale recorded by moss

Gaillard et al. (1994) showed that moss polsters are likely to record a pollen spectrum from a very small and local area, often reflecting only one land-use type. von Stedingk et al. (2008) showed that the relevant source area of pollen (RSAP) from forest tundra ecotone is approximately 500 m and Broström et al. (2005) showed it is 400 m for Swedish open and semi-open landscapes. As it applied to Swiss pasture woodlands, the study from Mazier et al. (2008) is of particular interest for us: they showed that RSAP from moss polsters in pasture woodlands have a 300 m radius. All of our study sites were at least 500 m distant from each other, and only 7 pairs of sites were less than 1 km distant, except the pairs P1<sub>b</sub>/P2<sub>a</sub> and P0<sub>b</sub>/P1<sub>c</sub> (170 and 420 m, respectively). Nevertheless, cluster analyses based on pollen assemblages did not set the stations from these pairs close to from each other. Our results thus suggest that the signal recorded by the herb pollen spectra corresponds to a finer spatial scale than that of the woody species. The same questions also apply to NPPs, but very few studies attempted to define the “relevant source area of NPPs”, and it remains a major lack of knowledge (Cugny et al., 2010; Cugny, 2011).

The time span recorded by moss samples is also an important point to discuss. Mulder and Janssen (1999) found that moss polsters can live 10 to 30 years long according to radio-caesium dating, while Crowder and Cuddy (1973) suggested 5 to 15 years. Bradshaw (1981) estimated that the green part of moss is likely to record 5 years of pollen deposition, but Cundill (1991) showed that the growing part would represent only few months. However, he agreed with Caseldine (1981) who stated that the complete moss polster records at least 2 years of pollen rain. As other studies also showed that moss samples are likely to record one to five years of rain deposit



(Räsänen et al., 2004; Pardoe et al., 2010), there is a general agreement to consider epigeic moss polsters as able to record at least one (often two) year of pollen production.

#### 5.4. Framework for the interpretation of fossil records

As a main objective, this study has been carried out in order to identify modern analogs and local indicators so as to provide a frame of reference for the fossil pollen rain recorded in Lake Saint-Point (Leroux et al., 2008). Applying the modern analog method using our data would have to be done carefully when our results will be compared with past pollen records. A potential bias could for instance appear in grazed wetlands. First, unlike other categories, they could not be distributed all around Lake Saint-Point but mostly on its western side because of wetland locations. Second, pollen spectra from grazed wetlands showed that they were likely to overestimate the proportions of tree and shrubs pollen taxa. Furthermore, the lake's catchment is 247 km<sup>2</sup> wide and stretched out toward the southwest, far away from the area where we took our moss samples. Lacustrine sequences usually collect local, regional and long-distance transport as well as inwash of mixed ages from the catchment, while moss samples represent highly local pollen and NPP spectra. Deep lacustrine samples from the water/sediment interface could be sampled in order to be compared to moss cushion analyses (Wilmschurst and McGlone, 2005; Parker and Williams, 2012).

Finally, RV-coefficients showed that there are no strong relationships between arboreal pollen and their corresponding species, and confirmed that the reconstructions of past vegetation based only on the analysis of the AP/NAP ratio cannot be sufficient (Cour et al., 1999; Court-Picon et al., 2005). Although some comparison with fossil pollen samples (by clustering methods) that we already performed showed that our most wooded sites were grouped together with highly wooded early medieval periods (before 1000 AD), we need to better investigate this question to provide an efficient tool to help interpretation of fossil data from Lake Saint-Point or other past middle mountain wooded-pasture landscapes.

## 6. Conclusion

This study provides new modern pollen and NPP rain and current vegetation relevés from middle mountain pasture woodlands. We applied original statistical analyses in order (1) to address the relationships between these two datasets, (2) identify the local modern pollen/NPP analogs in order to constitute a frame of reference for the palynological sequence from Lake Saint-Point. The analysis of our results emphasized several promising findings but also underlined some limits.

1. We confirmed the usefulness of multivariate tools to investigate complex datasets involving species variables in response to environmental variables, and more specifically to assess the link between vegetation and pollen spectra. While most palynological studies resort to Principal Components Analysis (PCA) or Canonical Correspondence Analysis (CCA) to address these questions, we applied Multiple Factor Analysis (MFA) and Redundancy Analysis (RDA). MFA was used to compute RV coefficients, which proved to be very useful to investigate the relationships between several groups of variables and, consequently, to investigate pollen–NPP–vegetation relationships and environmental variables. Second, we chose RDA (after Hellinger transformation) rather than CCA because of its robustness regarding rare species (Borcard et al., 2011). Although the original methods we showed here are reliable, the community of palynologists needs to apply them to different datasets to better understand their limits. However, MFA and RDA produced interesting results, and their ability to reveal some taxa as tree cover or grazing indicators in agreement with previous

studies is a good argument in favor of their reliability and we encourage palynologists to consider them.

2. This study confirmed the indicative power of some taxa, such as coprophilous fungi, more specifically *Sporormiella* (HdV-113), which showed a negative correlation to tree cover and a strong link to dung samples. *Trichocladium* (HdV-572), well known to frequently occur in beech forests (Cugny et al., 2010) and *Cirrenalia* were well represented in our most wooded sites, although coniferous taxa (*Abies alba* and *Picea abies*) are the main contributors to tree cover. This study also confirmed pollen taxa such as *Trifolium repens*-type, *Trifolium pratense*-type, *Plantago major/media*-type and *Plantago lanceolata*-type as grazing indicators, and arboreal taxa such as *Picea*, *Abies*, *Fagus* and *Corylus* as the main tree cover indicators among the pollen taxa.
3. In addition to these confirmations, we also identified a diverse group of potential new NPPs as indicators of tree cover, grazing pressure or openness. LCE-13 can be interpreted as an openness indicator and might be a grazing indicator as well, despite a small occurrence in one ungrazed site. As for LCE-23, its high abundance in unwooded pastures and its absence from most wooded sites allowed identifying it as a grazing pressure indicator. This could also be the case for LCE-32 even though it was not present in enough plots to establish a strong correlation. Nevertheless, this is a promising original result and we hope that further studies confirm some of these taxa as coprophilous fungi, or at least as grazing pressure indicators.
4. Our results support the possibility to derive an extant plant community from the analysis of the pollen grains it produces, in agreement with previous studies dealing with pollen–vegetation relationships (e.g. Gaillard et al., 1994; Court-Picon et al., 2005; Soepboer et al., 2010), but also from associated NPPs. This study contributes in filling a gap in palynological data from mountainous areas, more specifically in pasture woodlands, and provides a framework for past vegetation and land-use reconstruction around Lake Saint-Point. However the use of our data from moss and dung samples to interpret lacustrine records will have to be applied carefully knowing their inherent differences according to spatial and temporal record scales and deposit mechanisms.

Although this represents only a first step and deeper investigations are needed, we are enthusiastic about further use of our results and we believe that they will help in the interpretation of fossil pollen and NPP records of the area, and from similar pasture woodland landscape as well.

## Conflict of interest statement

We noticed no conflict of interest that could affect the author and co-authors of this study.

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## Appendix A. Excluded taxa from moss sample diagram

Data are expressed in percentages relatively to the pollen sum (all pollen taxa excluding Cyperaceae and Poaceae) (HdV: Hugo de Vries Laboratory, Amsterdam, The Netherlands; TM: University Toulouse-le Mirail, Toulouse, France; LCE: Chrono-Environment Laboratory, Besancon, France).

Vegetation type	Grazed wetlands			Unwooded pastures			Sparsely wooded pastures			Densely wooded pastures			Grazed forests			Ungrazed forests		
Site ID	W <sub>a</sub>	W <sub>b</sub>	W <sub>c</sub>	P0 <sub>a</sub>	P0 <sub>b</sub>	P0 <sub>c</sub>	P1 <sub>a</sub>	P1 <sub>b</sub>	P1 <sub>c</sub>	P2 <sub>a</sub>	P2 <sub>b</sub>	P2 <sub>c</sub>	P3 <sub>a</sub>	P3 <sub>b</sub>	P3 <sub>c</sub>	F <sub>a</sub>	F <sub>b</sub>	F <sub>c</sub>
<i>Acer</i>	0.2	0	0.7	0	0	0	0.6	0	0.4	0.3	0	0.6	0.2	1.1	0	0.7	0	0.4
<i>Alnus</i>	1.3	1.1	1.3	0	0	0.4	1.9	0.3	1.5	0.9	2.2	1.6	0.2	1.9	1	1.7	2.8	1.2
<i>Castanea sativa</i>	1	0	2	0	1.1	0	0.3	0	0.7	0	0.6	0	0.4	0.5	0.2	0.4	0	0
<i>Fraxinus</i>	0.8	1.4	0	0	2.1	0.4	2.2	4.4	2.2	1.5	3.8	1.4	0.4	2.8	1.4	1.1	2	1
<i>Juglans</i>	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0.3	0	0.2	0.3	0.2
<i>Salix</i>	0.5	0	0.3	0	0	0	0	1.2	0.4	0.3	1.1	0.4	0	0.3	1.6	0	1.1	0.6
<i>Sorbus-group</i>	0	0	0	0	0.7	0.4	1.9	0	0.4	0	0.8	0.2	0	0.5	0	0.4	0.3	0
<i>Tilia</i>	0.2	0	0	0	0	0	0.6	0.3	0	0	0	0.4	0	0.3	0	0	0	0.2
<i>Ulmus</i>	0.2	0.3	0	0	0	0	0	0.6	0.4	0	0.6	0	0	0.5	0.2	0.2	0	0
<i>Buxus</i>	0.5	0	0.7	0	0	0.4	0	0	0.4	0.3	0.6	0.2	0	0	0	0.4	0.3	0.2
<i>Frangula alnus</i>	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hedera helix</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0
<i>Ilex aquifolium</i>	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0
<i>Juniperus</i>	0.2	0	0	0	0	0	0	0	0.4	0	0.3	0	0.2	0	0	0	0	0
<i>Lonicera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0.2	0	0	0
<i>Loranthus europaeus</i>	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sambucus nigra-type</i>	0	0	0	0	0	0	0	0	0.7	0	0	0	0	0	0	0	0	0
<i>Viburnum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0
<i>Vitis</i>	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0
<i>Artemisia</i>	0.2	0	0.3	0	0	0	0.3	0	0	0	0	0	0.2	0.3	0	0	0	0.4
<i>Astragalus-type</i>	0	0	0	0	0	0.4	0	0	0	0	0.3	0	0	0	0	0	0	0.2
Brassicaceae	1.3	0.3	2.3	0	0.3	0	0	0	0.4	0.9	1.3	1	0.2	0.5	0	1.5	0.3	1
<i>Calystegia</i>	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0
Campanulaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0
<i>Centaurea jacea-type</i>	0.2	0	0	0	0.7	0	0	0	0.4	0	0	0	0	0	0	0	1.1	0.2
Cerealia type	0	0	0	0	0	0	0	0.3	0	0.3	0.6	0.2	0	0	0.4	0.2	0.3	0.2
Chenopodiaceae	1.3	0	0.7	0	0.3	0	0	0.6	0.7	0	0.3	0.2	0.2	0.3	0	0.6	0.3	0.2
<i>Cirsium-type</i>	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dipsacaceae	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0
<i>Equisetum</i>	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ericaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0
Euphorbiaceae	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0
<i>Gentiana pneumonanthe-type</i>	0	0	0	0	0	0	1.6	0.3	0	0	0	0.6	0	0	0	0	0	0
Gentianaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0
Geraniaceae	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heracleum-type</i>	0.8	0	0	0	0	0	0.3	0	0	0	0.8	0.6	0.2	0	0	0.4	0.6	0.2
<i>Hypericum perforatum-type</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0
<i>Lathyrus-type</i>	0	0	0	0	0.7	0	0	0	0	0.3	0	0	0	0	0	0	0	0
<i>Linaria-type</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0
<i>Lotus-type</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0
<i>Lysimachia vulgaris-type</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0
Papaveraceae	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0
<i>Polygonum aviculare-type</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0
<i>Polygonum bistorta-type</i>	0	1.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Potamogeton natans-type</i>	10.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhinanthus-group</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0
Rosaceae	0	0	0	0	0	0	0	0	0.7	0	0	0	0.6	0	0	0	0	0
<i>Rubus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0.3	0.4
<i>Salvia pratensis-group</i>	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0
<i>Sanguisorba minor-type</i>	0	0	0.7	2.4	0	0	0.6	1.6	0.7	0.6	0	0.2	1.2	0.8	0.2	0	0	0.2
Scrophulariaceae	0	0	0	0	0	0	0	2.5	0	0.3	0	0	0	0	0	0	0	0
<i>Silene-type</i>	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2
<i>Sparganium-type</i>	0.8	0	0	0	0	0	0	0.3	0	0	0.3	0	0	0	0	0	0	0.2
<i>Thalictrum</i>	0	0.3	0	0	0.3	0	0	0	0	0	0	0	0	0	0.2	0	0	0
<i>Typha latifolia-type</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0
Urticaceae	0	0	1	0	0	0.4	0.6	2.8	1.1	0.3	0.6	0	0.2	0.3	0.8	0	0	0
Valerianaceae	0.2	0.3	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0
<i>Xanthium spinosum-type</i>	0.5	0	1.6	0	0	0	0.3	0.6	0	0.6	0.3	0	0	1.1	1	0.2	0.6	0.2
<i>Amphisphaerella dispersella</i> (HdV-310)	0.2	0	0	0	0	0	0	0.5	1.8	1.9	0	0	0.1	1.5	0.4	0	0	0
<i>Byssothecium circinans</i> (HdV-16)	0	0	0	3.2	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0
<i>Chaetomium</i> (HdV-7A)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0.3	0	0	0
<i>Clasterosporium caricinum</i> (HdV-126)	0	0.6	0.9	3.2	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coniochaeta ligniaria</i> (HdV-172)	0	0	0	0	1.9	0.5	0.4	0	0	0	1.4	0.1	0	0.5	0.1	0	0	0
<i>Dictyosporium</i> (HdV-498)	0	0	0	0	0	0	0	0	0	0.2	0	0.3	0	0	0	0	0	0
<i>Didymosphaeria</i> (HdV-85)	0	0	0	0	0	0	0	2.9	0.7	0	0	0	0	0	0	0	0	0

(continued on next page)



Vegetation type	Grazed wetlands			Unwooded pastures			Sparsely wooded pastures			Densely wooded pastures			Grazed forests		
Site ID	W <sub>a</sub>	W <sub>b</sub>	W <sub>c</sub>	P0 <sub>a</sub>	P0 <sub>b</sub>	P0 <sub>c</sub>	P1 <sub>a</sub>	P1 <sub>b</sub>	P1 <sub>c</sub>	P2 <sub>a</sub>	P2 <sub>b</sub>	P2 <sub>c</sub>	P3 <sub>a</sub>	P3 <sub>b</sub>	P3 <sub>c</sub>
Brassicaceae	0.6	0	0	0	0	0.6	0	0	0	0	0	0	0	0	0
Campanulaceae	0	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0	0
<i>Centaurea cyanus</i>	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0
<i>Cerealia</i> -type	0	0	0	1.3	0	0.3	0	0	0	0.5	0.5	0	4.7	0	0.4
Chenopodiaceae	0.6	1.2	1.1	0	0	0	0	0.4	0	1.4	0	0	0	0	0
<i>Cirsium</i> -type	0	0.6	0.7	0	0	0	0	0	0	0	1.8	0	0	0	0
Dipsacaceae	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0
Euphorbiaceae	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0
Geraniaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2
<i>Helianthemum</i>	0	0	0	0	0	0	0.3	0.9	0	0	0	0	0	0	0
Lamiaceae	0	0.6	0	0	0	0	0.9	0	0	0	0	0.2	0	0	0.8
<i>Lathyrus</i> -type	0	0	1.1	0	0.9	0.3	0.9	0.4	0	0	0	0	0.8	0	0
<i>Lotus</i> -type	0	0	0	0	0	0.3	5.5	0.4	0.4	0.5	0	0	0	0.4	0.6
<i>Polygonum aviculare</i> -type	0	1.7	1.1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Potentilla</i> -type	1.2	0	0	0	0	0	0.9	0.9	1.9	1.9	0.5	0	0.8	0	0
<i>Rhinanthus</i> -group	0	0	0	0	2.3	0	0.3	1.9	0	0	0	0	0	0	0.2
Rosaceae	0	0	0	0	0	0	0	0	0	0	0	0	0.8	0	0
<i>Rubus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1.6	0	0
<i>Salvia pratensis</i> -group	0	0	0.4	0	0.9	0	0.3	1.4	0	0.9	0	0	0	0	0
<i>Sanguisorba minor</i> -type	0	0	0.4	0.4	0	0	0	1.9	0	2.8	0.5	0	0	0.4	0.6
<i>Silene</i> -type	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0.2
<i>Succisa</i> -type	0	4.7	0	0	0	0	0	0	0	0	0	0	0	0	0
Urticaceae	1.8	0	0	0	0.4	0	1.2	0.4	0	0	0	0.5	0	0	0
Valerianaceae	0	0.6	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Xanthium spinosum</i> -type	0.6	1.2	1.1	0	0.4	0	0	0	0.4	0	0.5	1	0	0	0
<i>Amphisphaerella dispersella</i> (HdV-310)	0	0	0	0.3	0	0	1	0	0	0	0	0	0	0	0
<i>Byssothecium circinans</i> (HdV-16)	0	0	0	0	0.6	0	0	0	0	0	0	0	0	0	0
<i>Chaetomium</i> (HdV-7A)	0	0	0	0.3	0	0	0	0	0	0	0.4	0	0	0	0
<i>Cirrenalia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0
<i>Clasterosporum caricinum</i> (HdV-126)	0	2.3	1.4	0	0	0	0	0	0	0.8	0	0.9	0	0	0
<i>Coniochaeta</i> cf. <i>lignaria</i> (HdV-172)	0	0.8	0	0	0	0	0	2.4	0	0.8	1.1	0	0	0	0
<i>Didymosphaera</i> (HdV-85)	0	0	0	0	0	0	0	0.9	0	0	0.4	0.4	0	0	0
<i>Diporotheca</i> (HdV-143)	0	0	0	0	1.9	0	0	0	0	0	0	0	0	0	0
<i>Gelasinospora</i> cf. <i>reticulispora</i> (HdV-2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0
<i>Geoglossum sphagnophilum</i> (HdV-77A)	0	0	0	0	0.6	0	0	0	0	0	0	0	0	0	0
<i>Herpotrichiella</i> sp. (HdV-22)	0	0.8	0	0	0	0.9	0	0	0	0	0	0	0	0	0
<i>Meliola</i> cf. <i>niessleana</i> (HdV-14)	0	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Monoletes</i>	0	0	0	0	0	0.9	0	0.9	0	0	0	0	0	0	0.1
<i>Saccobolus</i>	0	0	0	5.5	0	0	0	0	0	0	0	0	0	0	0
<i>Thecaphora</i> sp. (HdV-364)	0	0	0	0	0	0	0	0.9	0	0	0	0	0	0	0
<i>Trichoglossum</i> cf. <i>hirsutum</i> (HdV-77B)	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0
<i>Triposporium</i> (TM-M1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	0
<i>Valsaria</i> sp.	0	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0
HdV-7B	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0
HdV-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0
HdV-85	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0
HdV-200	0	0	0.2	0	0	0	1	0	0	0	0.4	47.8	0	0	0
HdV-205	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0
HdV-351	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0.1	0
HdV-364	0	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0
LCE-14	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0
LCE-18	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0
LCE-19	0	0.8	0	0.3	0	0	0	0	0	0	0.4	0	0	0	0
LCE-21	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
LCE-25	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0
LCE-26	0	0	0	0	0	0	0	0	1.3	0.8	0	0	0	0	0
LCE-31	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
LCE-33	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0



For trees and shrubs, numbers represent absolute percent cover of each species derived from Braun-Blanquet's dominance code in each 400-m<sup>2</sup> plot. For herbaceous species, numbers represent absolute percent frequency of each species in ten 0.25-m<sup>2</sup> quadrats per site.

	Vegetation type	Grazed wetlands			Unwooded pastures			Sparsely wooded pastures			Densely wooded pastures			Grazed forests			Ungrazed forests			
	Site ID	W <sub>a</sub>	W <sub>b</sub>	W <sub>c</sub>	P0 <sub>a</sub>	P0 <sub>b</sub>	P0 <sub>c</sub>	P1 <sub>a</sub>	P1 <sub>b</sub>	P1 <sub>c</sub>	P2 <sub>a</sub>	P2 <sub>b</sub>	P2 <sub>c</sub>	P3 <sub>a</sub>	P3 <sub>b</sub>	P3 <sub>c</sub>	F <sub>a</sub>	F <sub>b</sub>	F <sub>c</sub>	
Trees	<i>Abies alba</i>													65	20			90	75	
	<i>Corylus avellana</i>													20		12				
	<i>Crataegus monogyna</i>												10							
	<i>Fagus sylvatica</i>													3		15	30		5	
	<i>Fraxinus excelsior</i>										10	30				2				
	<i>Picea abies</i>							40	40	15	40	30	50		70	80	90			
Shrubs	<i>Sorbus aucuparia</i>										4				2					
	<i>Abies alba</i>								1		1		3		10	20	8			
	<i>Acer pseudoplatanus</i>							1						1		1			1	
	<i>Corylus avellana</i>							1	1	1	25	10	6	4	15	3		4	7	
	<i>Crataegus laevigata</i>										3	1		1						
	<i>Crataegus monogyna</i>							1	10	5	3	7	5	1		10				
	<i>Fagus sylvatica</i>										1	3	1		10		3		6	
	<i>Fraxinus excelsior</i>										1	3				1		1	1	
	<i>Juniperus communis</i>							8			6		1							
	<i>Ligustrum vulgare</i>											1								
	<i>Lonicera nigra</i>																			
	<i>Lonicera xylosteum</i>										2				4			4	17	
	<i>Picea abies</i>										3	2	1	2	6	3	4	4	4	4
	<i>Prunus padus</i>												1							
	<i>Pyrus pyraister</i>												8	2						
	<i>Ribes alpinum</i>									1										
	<i>Rosa arvensis</i>					1						1	2			1	1		1	1
	<i>Rosa canina</i>															1		2		
	<i>Rubus fruticosus</i> aggr.																			
	<i>Salix cinerea</i>			2	2							1	2		1				2	60
	<i>Sambucus nigra</i>																			
	<i>Sambucus racemosa</i>																			
	<i>Sorbus aria</i>																			
	<i>Sorbus aucuparia</i>											1	2	1	1	2		1		
	<i>Viburnum lantana</i>											1			1	1		1	3	1
	<i>Viburnum opulus</i>											1	1	1				1		
	Herbs	<i>Abies alba</i>													10	40	20	20	50	10
		<i>Acer pseudoplatanus</i>																		
		<i>Achillea millefolium</i>				60	60	20	10	80	10	20		20						
		<i>Agrostis capillaris</i>	40	10	10		20	20	20	20	20		40	20	40					
		<i>Ajuga reptans</i>	70		30	10	30	50	20	10	50	70	10	10	20	50	30		20	50
		<i>Alchemilla monticola</i>			10	50	20	10	10	40	30	40	30	30	40					
<i>Alchemilla xantochlora</i>							10									10				
<i>Alopecurus pratensis</i>																				
<i>Angelica sylvestris</i>				50																
<i>Anthoxanthum odoratum</i>				40																
<i>Anthriscus sylvestris</i>										10										
<i>Anthyllis vulneraria</i>												10								
<i>Asarum europaeum</i>																	40		20	40
<i>Athyrium filix-femina</i>																				10
<i>Briza media</i>				10																
<i>Campanula rotundifolia</i>									20	10		40		20	20					
<i>Cardamine hirsuta</i>			10																	
<i>Cardamine pratensis</i>				20	20															
<i>Carex elata</i>			40																	
<i>Carex flacca</i>			30	60	40				60	40	10	30		50	20	10		20		
<i>Carex rostrata</i>				20	30															
<i>Carex sylvatica</i>												10		10	50		30		10	30
<i>Carpinus betulus</i>																		10		
<i>Carum carvi</i>						30	80	80		80	90									
<i>Centaurea jacea</i>						10														
<i>Cerastium fontanum</i> <i>triviale</i>						10				10										
<i>Cirsium arvense</i>							10				10									
<i>Cirsium palustre</i>				50	40															
<i>Colchicum autumnale</i>													10							
<i>Corylus avellana</i>													10			20				
<i>Crataegus laevigata</i>												10								
<i>Crataegus monogyna</i>									10	20					10		10			
<i>Cynosurus cristatus</i>						50	80	80	10	50	60	40	20	10						
<i>Dactylis glomerata</i>						60		70	60	40	20	10	60	30		10				
<i>Dactylorhiza maculata</i>												10								
<i>Epilobium montanum</i>															10					
<i>Epilobium palustre</i>				30	10															

## Appendix C (continued)

Vegetation type		Grazed wetlands			Unwooded pastures			Sparsely wooded pastures			Densely wooded pastures			Grazed forests			Ungrazed forests		
Site ID		W <sub>a</sub>	W <sub>b</sub>	W <sub>c</sub>	P0 <sub>a</sub>	P0 <sub>b</sub>	P0 <sub>c</sub>	P1 <sub>a</sub>	P1 <sub>b</sub>	P1 <sub>c</sub>	P2 <sub>a</sub>	P2 <sub>b</sub>	P2 <sub>c</sub>	P3 <sub>a</sub>	P3 <sub>b</sub>	P3 <sub>c</sub>	F <sub>a</sub>	F <sub>b</sub>	F <sub>c</sub>
Herbs	<i>Equisetum palustre</i>			40															
	<i>Euphorbia dulcis</i>											10							
	<i>Festuca rubra</i> aggr.	80	50	60	70	20	90	40	80	50	60	60	60	50	40				
	<i>Filipendula ulmaria</i>	20	70	80															
	<i>Fragaria vesca</i>							60	30	20	60	70	30	60	80	30	20	40	60
	<i>Fraxinus excelsior</i>										60	30			10				
	<i>Galeopsis tetrahit</i>							10									10		
	<i>Galium album</i>			60	70			20	20		10		10	30					
	<i>Galium aparine</i>		40	40															
	<i>Galium odoratum</i>													20	10	30	30	70	100
	<i>Galium palustre</i>	50		50															
	<i>Galium pumilum</i>												20						
	<i>Galium rotundifolium</i>		60	60	10				10		20			30	40				
	<i>Galium uliginosum</i>	30																	
	<i>Galium verum</i>		20	40	90			30	20										
	<i>Gentiana lutea</i>			10				20					20						
	<i>Geranium robertianum</i>										10	40		10	30	10	20	80	50
	<i>Geum rivale</i>		60	40															
	<i>Heracleum sphondylium</i>					50	10					30							
	<i>Hieracium murorum</i>										30			20	70				
	<i>Hieracium pilosella</i>	30	40	10			10		10	30	50			20	10	20			
	<i>Hippocrepis comosa</i>										10								
	<i>Holcus lanatus</i>			20			10												
	<i>Hordelymus europaeus</i>											10			30		40	20	
	<i>Hypericum hirsutum</i>															10			
	<i>Hypericum humifusum</i>													20					
	<i>Hypericum montanum</i>								10						10				
	<i>Hypericum perforatum</i>												20						
	<i>Juncus alpino-articulatus</i>	100																	
	<i>Juncus effusus</i>		50	20															
	<i>Juncus tenageia</i>			40															
	<i>Lamium galeobdolon montanum</i>											10			10		10	30	
	<i>Lathyrus pratensis</i>		10	30	80		50	60	30		20	20	20						
	<i>Lathyrus sylvestris</i>																	40	
	<i>Lathyrus vernus</i>								20						20	20	10		
	<i>Leucanthemum vulgare</i>						40		10				20	10					
	<i>Linaria vulgaris</i>								10				10	20	10				
	<i>Lolium perenne</i>				70	40	10			20									
	<i>Lonicera xylosteum</i>										40			20	10				10
	<i>Lotus corniculatus</i>			20	60		10	20	40		20		20	10					
	<i>Maianthemum bifolium</i>																	10	
	<i>Melampyrum sylvaticum</i>														20				
	<i>Mentha aquatica</i>	20																	
	<i>Mercurialis perennis</i>															20	40	30	60
	<i>Moerhingia trinervia</i>										20								
	<i>Ononis spinosa</i>						10												
	<i>Oxalis acetosella</i>													20	30	50	30	100	100
	<i>Parnassia palustris</i>												20						
	<i>Phleum pratense</i>					60	10			40		20							
	<i>Picea abies</i>										10	10	10					50	
	<i>Plantago lanceolata</i>				100	40	80	30	40	10	10		30						
	<i>Plantago major</i>			20		60	20		10	60	10		30	20					
	<i>Plantago media</i>					30	20			10									
	<i>Polygonatum odoratum</i>														30				
	<i>Polygonatum verticillatum</i>														10	10	20	10	
	<i>Potentilla aurea</i>												10						
	<i>Potentilla erecta</i>		60	40				10			50		20	60					
	<i>Primula elatior</i>								20		20		10						
	<i>Prunella vulgaris</i>												10						
	<i>Ranunculus acris</i>			10	10							20		20					
	<i>Ranunculus acris friesianus</i>				90														
	<i>Ranunculus ficaria bulbifer</i>	60	10	60							50								
	<i>Ranunculus montanus</i>							50											
	<i>Ranunculus nemorosus</i>	100	50	50		80	100		90	80	60	40	80	70					
	<i>Ranunculus repens</i>	70		20	20	20	20	10		70	20								
	<i>Ribes alpinum</i>							10				10							
	<i>Rosa arvensis</i>																10		
	<i>Rubus fruticosus</i> aggr.													20		30	10		30
	<i>Rubus idaeus</i>												10						
	<i>Rumex acetosa</i>		20	30		30	30	30				10	20			10			
	<i>Sanguisorba minor</i>				50		10	20	70	10	60		30	10					
	<i>Sanguisorba officinalis</i>		20	30															
	<i>Scabiosa columbaria</i>												20						

(continued on next page)

Appendix C (continued)

Vegetation type	Grazed wetlands			Unwooded pastures			Sparsely wooded pastures			Densely wooded pastures			Grazed forests			Ungrazed forests			
	Site ID	W <sub>a</sub>	W <sub>b</sub>	W <sub>c</sub>	P0 <sub>a</sub>	P0 <sub>b</sub>	P0 <sub>c</sub>	P1 <sub>a</sub>	P1 <sub>b</sub>	P1 <sub>c</sub>	P2 <sub>a</sub>	P2 <sub>b</sub>	P2 <sub>c</sub>	P3 <sub>a</sub>	P3 <sub>b</sub>	P3 <sub>c</sub>	F <sub>a</sub>	F <sub>b</sub>	F <sub>c</sub>
<i>Sedum acre</i>						10													
<i>Senecio jacobaea</i>			10			30													
<i>Sorbus aria</i>												10						10	
<i>Sorbus aucuparia</i>															20	10			
<i>Stellaria media</i>								10											
<i>Succisa pratensis</i>			20																
<i>Taraxacum officinale</i> aggr.				10	50	70	100		90	60				10					
<i>Taraxacum palustre</i>	10																		
<i>Thymus pulegioides</i>			10							10	20		10						
<i>Trifolium dubium</i>							20												
<i>Trifolium pratense</i>	60	10	30		90	100	100	60	80	100	10	40	10	10					
<i>Trifolium repens</i>					100	10	60	10			40		60	30				10	
<i>Triglochin palustris</i>	50																		
<i>Vaccinium myrtillus</i>																	30	20	20
<i>Valeriana dioica</i>			60																
<i>Veronica chamaedrys</i>	10	10			90	10	70	60	70	30	60	90	30	50		20			
<i>Veronica officinalis</i>											50		30	20	10	20		20	10
<i>Viburnum opulus</i>																10			
<i>Vicia cracca</i>			10	70	20		60	10											
<i>Vicia sepium</i>								30	10	10	10	10	30	10		10		10	10
<i>Viola hirta</i>					10								10	30					
<i>Viola riviniana</i>												30							20
<i>Viola reichenbachiana</i>									10			20	20		30	60	70	20	30

Appendix D. Morphological description of potential new NPPs found in moss and dung samples from pasture woodlands around Lake Saint-Point (Doubs, France)

LCE-12 (Fig. 8k)

Small microfossil, light brown, kidney-shaped, 15 µm long, with two small apertures on extremities. Found only in moss samples from grazed sites.

LCE-13 (Fig. 8l)

Discoid microfossil, light brown, 13 µm width, flat, with small aperture (porous?) aside. Present in all kinds of samples and stations.

LCE-14

Light brown microfossil, egg-shaped, 18 µm long and 12 µm width, with small aperture by one third of main axis, by the apex-side. Not found in dung samples, not found in samples from wet sites and not found in moss samples from ungrazed forests.

LCE-15 (Fig. 8v)

Brown microfossil composed by a rugulate spherical center (30 µm diameter) from which long spines start (up to 35 µm long). Spines usually grouped by pairs of two spines closer to each other than with the other. Not found in dung samples.

LCE-16

Globose microfossil, light brown, 23 µm diameter, with five grouped apertures. Found only in one moss sample from grazed forest.

LCE-17

Egg-shaped microfossil, 23 µm long. Found only in moss samples from grazed sites.

LCE-18

Rectangular microfossil, 18 µm long and 5 µm width with thick wall (almost 1 µm width) and one aperture on one of the small face. Found only in grazed sites but not in wetlands.

LCE-19

Microfossil 13 µm long with one protuberance in the middle of the main axis and an aperture (not protruding) on the other side.

LCE-20

Brown microfossil, one septate with body constriction around the septum, 70 µm long and 32 µm width, with protuberance on extremities. Possibly *Valsaria variospora* (HdV-140). Found only in moss sample from one unwooded pasture.

LCE-21

Small microfossil, 10 µm long and 5 µm width, with one constricted septate. Possibly a small specimen of type HdV-85.

LCE-22 identified as *Cirrenalia* (Fig. 8f)

Curved pluri-septate microfossil, 22 µm diameter. Found in moss samples except a small occurrence in a dung from grazed forest.

LCE-23 (Fig. 8a)

Sinuuous microfossil, 30 µm long but seems to extend, often groups by dozens around a spherical support. Found in almost all stations except ungrazed forests and in high amounts among dung samples.

LCE-24 (Fig. 8c)

Brown microfossil, one septate with body constriction around the septum, 70 µm long and 32 µm width, with protuberance on extremities. Possibly *Valsaria variospora* (HdV-140) or LCE-10. Found only in moss sample from one sparsely and one densely wooded pasture.

LCE-25

Kidney-shaped microfossil, similar to LCE-2 but 45 µm long, with apertures on extremities. Mostly found in mosses from grazed sites and one occurrence in the dung sample from one densely wooded pasture.

LCE-26 (Fig. 8n)

One-septate microfossil, with slightly constriction, 15 µm long and 10 µm width and thick wall (1–2 µm thick). Found in all kinds of

samples except dung from wetlands, but not found in unwooded pastures.

#### LCE-27 (Fig. 8r)

Dark brown microfossil, pluri-septate, with one spherical extremity darker than other segments. 45 µm long and 30 µm width, with aperture on the distal segment. Found only in moss from ungrazed forests.

#### LCE-28 identified as Dictyosporium (HdV-498) (Fig. 8p)

Light brown microfossil, 45 µm long and 25 µm width, consisting in a mass of globose cells, each from 5 to 10 µm diameter, arranged in two-dimension mosaic. Found only in moss samples from grazed sites.

#### LCE-29

Dark brown microfossil except on extremities, which are angled, one in the opposed direction of the other. One septate, with slight constriction. 45 µm long and 15 µm width. Only one small occurrence in a moss sample from an unwooded pasture.

#### LCE-30

Ring-shaped small light brown microfossil, 15 µm diameter, internal diameter 9 µm. Found only in moss sample from a grazed wetland.

#### LCE-31

Small cylindrical microfossil, with endless screw-like sculpture, 18 µm long and 6 µm width. Found only in a dung sample from a grazed wetland.

#### LCE-32

Light brown discoid microfossil, 16 µm diameter, similar to LCE-2 but without aperture. Found only on some dung samples, often in high amounts.

#### LCE-33

Multi-cells microfossils, about 100 µm long. Found only in a dung sample from one grazed forest. Possibly *Alternaria* (see McAndrews et al., 2010. Fungal spores record Iroquoian and Canadian agriculture in 2nd millennium A.D. sediment of Crawford Lake, Ontario, Canada. *Veget Hist Archaeobot* 19, 495–501.).

#### LCE-34

35 µm long and 30 µm width mass of 12 cells arranged in 3 rows of 4 cells, inner cells bigger than outer. Corner cells more rounded, others rectangular. Found only in a moss sample from one unwooded pasture.

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